Appl. Math. Lett. Vol. 3, No. 4, pp. 81–84, 1990
Printed in Great Britain.

0893-9659/90 \$3.00 + 0.00

Conflicting Density Dependent Dynamics of a Bacterial Population

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(Received June 1990)

Abstract. We consider how the antagonistic effects of dispersal, which takes place preferentially down a population gradient, and the tendency to group together governs the dynamics of dispersal of a population. We propose a model which considers these effects. The phase plane analysis and the numerical calculations reveal the existence of stable sharp wave front solutions.

INTRODUCTION

Based on a phenomenological random walk Montroll and West [1] proposed a nonlinear diffusion equation which can be extended to:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - 2\xi\frac{\partial}{\partial x}[gu\frac{\partial u}{\partial x}] + (K.T.), \tag{1}$$

where $D = a^2/2\tau - 2\xi g\, u$, being $\xi = \mu a^2/\tau$, and a is the length of each cell, τ is the duration of the pause between each step, μ is a coupling parameter, and g is an arbitrary weighting of u; $(K.T.)$ in eq. (1) stands for the growth terms. If the function $g(u)$ is set equal to a constant, then the bias depends only on the concentration gradient between sites. In the case when the bias could be less than the local concentration, for instance, 0.8 rather than 0.2, then a choice for the weighting function had the form [1]:

$$g(u(k,n)) = [1 - \beta u^{\alpha}(k,n) + \gamma u^{\alpha+1}(k,n)]/\alpha \tag{2}$$

From the postulated form of the random walk process the weighting function is interpreted in terms of a conflict in the dynamics, of attractive and repulsive interactions between the members of the population. In this weighting function β and γ are factors which weight the degree and type of interaction between the elements which constitute the system.

Since the pioneering work proposed by Cohen and Murray [2], the dynamics of populations with negative diffusivity have not been widely studied. The purpose of the present work is to extend previous reports [3,4] to study a conflicting dynamics which include negative diffusivity, and is based on the kind of interactions which the bacteria of a colony establish during migration. Other ways of considering aggregating tendencies have also been proposed in the literature [5,6,7,8,9]. For a wide discussion on density dependent dispersal of populations see the book of Murray [10], also ref. [11].

Given that, for bacteria, the interactions may change during the different stages of growth, it is also necessary to consider that the weighting parameters β and γ may be spatially dependent. Thus, ignoring any contribution from purely diffusive terms, the final form of the conservation equation is:

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}[\beta^*(r)u + \gamma^*(r)u^2]\frac{\partial u}{\partial x} + u(k_1^* - u), \tag{3}$$

where a logistic birth and death process is assumed for the rate of growth, and where its constants are now nondimensional.

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PHASE PLANE ANALYSIS AND NUMERICAL RESULTS

For the phase plane analysis of system (3), β and γ are considered to be constants. Thus, we looked for travelling wave solutions through the change of variable $n = x - ct$ for some constant $c \in R^+$. The resulting phase plane equations became:

$$\frac{du}{dn} = v; \qquad \frac{dv}{dn} = \frac{-(\beta + 2\gamma u)v^2 - cv - u(k_1 - u)}{(\beta u + \gamma u^2)} \tag{4}$$

There is a singularity for $u = 0$. Aronson [3] eliminated it by introducing a new independent variable using a transformation similar to:

$$\frac{d}{dn} = \frac{1}{(\beta u + \gamma u^2)} \frac{d}{dt} \tag{5}$$

The resulting equation is not singular and has critical points at:

$$(u_0, v_0) = (0,0); \quad (k_1, 0); \quad (0, -c/\beta); \quad (-\beta/\gamma, 0.5[c/\beta \pm (c^2/\beta^2 - (4/\gamma)(\gamma + \beta))^{0.5}]) \tag{6}$$

For $\beta > 0$ and $\gamma > 0$ only the first three steady states exist. In this case, heteroclines were found emerging from $(k_1, 0)$ which, for values of c in the range $0 < c < c^*$, connect with the steady state at $(0,0)$. For values of $c = c^*$ there exists a saddle-saddle connection with $(0, -c/\beta)$, which is also joined to the origin by a trajectory. This saddle-saddle heterocline corresponded to a sharp travelling wave. For values of $c > c^*$ trajectories from $(k_1, 0)$ tended to infinity.

For $\beta > 0$ and $\gamma < 0$ or for $\beta < 0$ and $\gamma > 0$ the five steady states given by (6) exist. In this case for $c < c^*$ the behaviour is similar to that described in the previous case. But, for $c = c^*$ the saddle-saddle connection is between $(k_1, 0)$ and $(-\beta/\gamma, 0.5[c/\beta - [c^2/\beta^2 - (4/\gamma)(\gamma + \beta)]^{0.5}])$, which corresponds to a sharp travelling wave (see Figure 1). This last steady state is also joined by a trajectory to the node $(-\beta/\gamma, 0.5(c/\beta + [c^2/\beta^2 - (4/\gamma)(\gamma + \beta)]^{0.5}))$. For $c > c^*$, an heterocline exists between $(k_1, 0)$ and the node next to the origin (Figure 1).

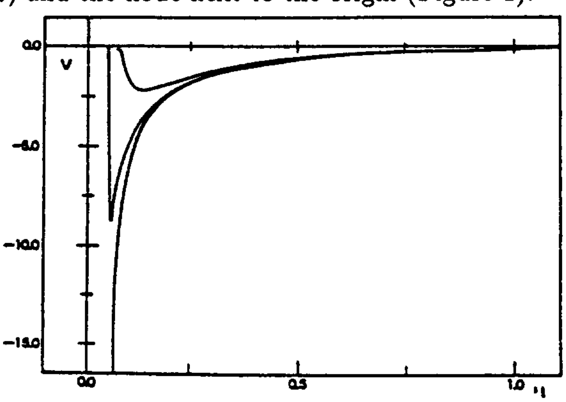


Figure 1. Phase plane diagram for system (7). For $c^* = 0.48085$ an heterocline joins the steady states (k_1 , 0) and ($-\beta/\gamma$, 0.5 (c/β - $[c^2 / \beta^2 - (4/\gamma)(\gamma + \beta)]^{0.5}$)). Moreover, this last steady state is joined by another heterocline to the stable node ($-\beta/\gamma$, 0.5 (c/β + $[c^2 /\beta^2 - (4/\gamma) (\gamma + \beta)]^{0.5}$)). For $c = 0.52 > c^*$ the heterocline diverges to infinity. Parameter values: $\beta = -0.025$, $\gamma = 0.333$, $k_1 = 1.0$.

For $\beta > 0$ and $\gamma = 0$, the value of c^* can be calculated from $c^* = k_1(0.5\beta)^{0.5}$. This result coincides with that previously reported in the literature [3] and [4]. For $\beta = 0$ and $\gamma > 0$, the value of c^* is in the range:

$$\gamma(\frac{4k_1 - 3}{6})^{0.5} < c^* < \gamma(\frac{3k_1 - 2}{3})^{0.5} \tag{7}$$

The procedure to estimate these bounds was proposed by Atkinson (1981). When both β and γ are greater than zero the value of c^* is larger than for the above cases. As we decrease the value of $\beta \longrightarrow 0$, the value of c^* decreases, until it approaches the bounded value for $\beta = 0$ given by (11). For $\beta > 0$, $\gamma < 0$ and keeping $\gamma < \beta$, the speed of propagation is smaller than for a case with the same value of β and with $\gamma = 0$. Taking $\beta < 0$, $\gamma > 0$ and maintaining $\beta < \gamma$, the decrease in speed is much more accentuated than for the previous case, and compared with the case using the same γ and $\beta = 0$. The restrictions on the relative values of β and γ are necessary because the stability of $(k_1, 0)$ changes, in the first case for values of $\gamma > \beta$ and in the second case for values of $\beta > \gamma$.

To test the stability of the sharp travelling waves, the PDE (3) was solved directly by numerical methods, using cartesian and polar coordinates. Perturbations of diverse magnitude were used as initial conditions. When perturbations of a magnitude smaller than the value of the steady state $(k_1, 0)$ were placed on the origin, they grew until they reached the value of the steady state, from where a wave front started moving (see Figure 2). By using initial conditions of larger magnitude than the steady state $(k_1, 0)$, the perturbations decreased towards this value, afterwards moving off as a propagation front. The same behaviour is observed in both types of coordinates with initial perturbations in different positions (Figure 2).

Stable travelling waves were obtained for different cases (Figure 2). For $\beta > 0$ and $\gamma < 0$ stable waves exist for γ from very small values until values slightly smaller than β. For $\beta < 0$ and $\gamma > 0$ stable waves were observed for different values of β, from very small values to values five times smaller than the value of γ. These results were obtained either using cartesian or polar coordinates. In general, no difference was observed between these two systems of coordinates, except for a slight decrease in the propagation speed seen with the polar coordinates, which was attributed to the effect of curvature.

All values of c^* were in agreement with those calculated from the phase plane analysis.

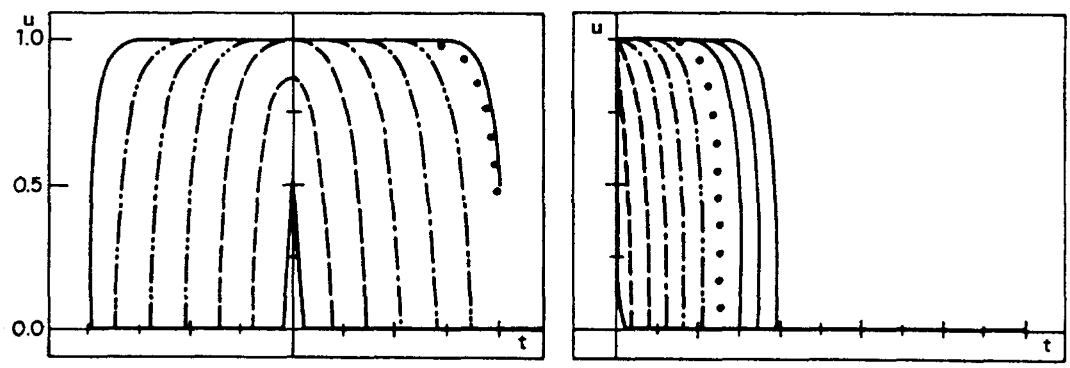
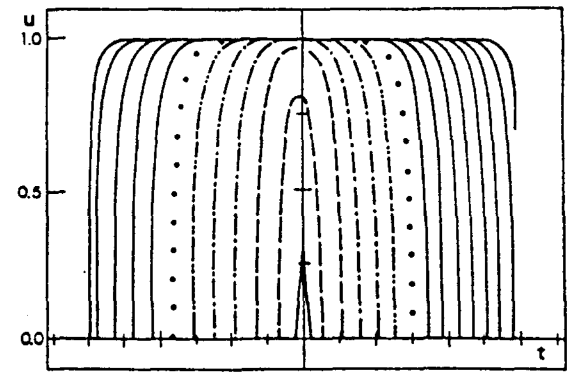


Figure 2. Travelling wave solutions using two different system of coordinates.
a) For cartesian, with initial conditions placed on the origin, $\beta = 0.5$, $\gamma = 0.333$, $c = 0.847$.
b) For polar coordinates $\beta = -0.005$, $\gamma = 0.333$, $c = 0.448$.

To include the spatial dependence of $\beta(r)$ and $\gamma(r)$, we assign to these parameters a linear dependence in space, from positive to negative values in the domain, using different slopes and magnitudes. In each calculation only one of the parameters was spatially dependent and the other one constant. In all the cases, the results show a gradual decrease in the propagation speed which became considerable over long periods of time (Figure 3).

In cultures of *E. coli* and *S. faecalis* it was observed that, in high glucose concentrations ($\leq 10g/l$), the radial growth was noticeably limited. This was attributed to substances secreted by the bacterium themselves [12]. The apparent similarity between this behaviour and the results of our model [13] suggest that aggregation dispersion tendencies among bacterium are possibly the very cause of the limitation. This has lead us to consider applying this approximation to other important ecological problems [14].

Figure 3. Travelling wave solutions with space dependent $\beta(r)$ and γ constant. There is a decrease in the speed of propagation for large times where $\beta(r)$ take negative values.



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